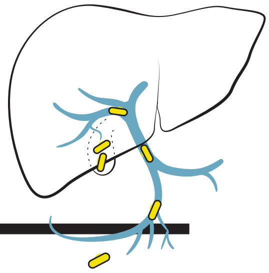
INSIGHTS

Snapshots of charge on the move p. 740

A gut-vascular barrier p. 742 ▸



PERSPECTIVES

EVOLUTION

One era you are in—the next you are out

Evolutionary trends in body size changed during a past mass extinction event

By **Peter J. Wagner**

Trends in body size are a rich source of information for evolutionary studies. This is because body size not only has numerous implications for function and life history but also has necessary limits that differ between groups of organisms. Moreover, there are many evolutionary patterns that might underlie trends, and these patterns need not be constant over time. On page 812 of this issue, Sallan and Galimberti (*1*) show that trends in the body sizes of vertebrates during the Devonian and Mississippian (about 420 to 325 million years ago) not only are markedly different at different times but also likely reflect a variety of different evolutionary mechanisms.

The Devonian shows a distinct trend toward larger vertebrates. This sort of trend often reflects a passive trend (*2*) (see the figure, panel A), where clades beginning near some limit (here, nearly as small as they can be) simply add variation in one direction (here, larger animals). However, Sallan and Galimberti present multiple lines of evidence that this reflects an active trend, where the new condition replaces rather than augments the existing condition (see the figure, panels B to D). In particular, their results suggest that driven trends (*3*), where descendants tend to be larger than their ances-

Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, USA. E-mail: wagnerpj@si.edu

Ancient sealife. Relatives of modern sharks and reef fishes that lived during the Mississippian (about 360 to 325 million years ago) reached sizes of up to 50 cm.

ILLUSTRATION: BOB NICHOLLS

tors (see the figure, panel B), predominate. Strong active trends toward increasing size are seen not just for all vertebrates but for five of the seven major taxonomic groups; one of the two exceptions (tetrapods) simply started out large.

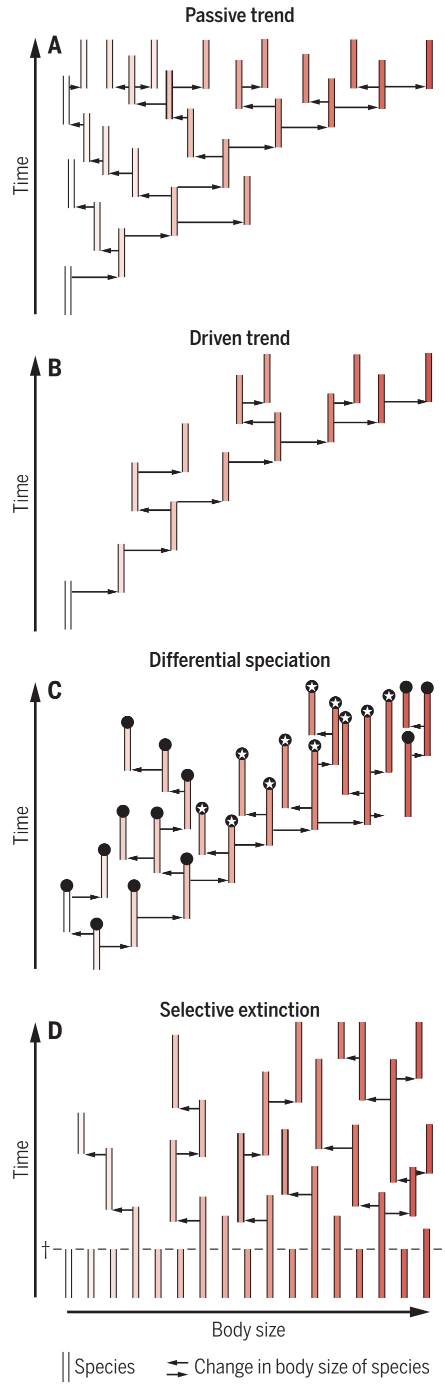
Breaking the trends down into finer taxonomic partitions reveals more heterogeneity. The clades showing no real trend tend to be those that begin fairly large, whereas most clades that start small show increases in size. This "subclade test" strongly suggests driven trends among a wide range of different vertebrates (*3*).

The end-Devonian mass extinction (~375 to 360 million years ago) reverses these trends. Three of the five surviving clades show marked decreases in body size. This indicates that selective extinction, at odds with prior selective forces (*4*), induces a new trend (see the figure, panel D). Devonian trends do not just fail to resume in the Mississippian; they are reversed, with a trend toward smaller size. However, whereas the Devonian trends include many groups, the Mississippian trends reflect two vertebrate groups. Chondrichthyans (elasmobranchs and holocephalans, the precursors of extant sharks and rays) are the only major group that shows evidence of driven trends toward smaller-bodied animals. Moreover, chondrichthyans also diversify in the Mississippian. Actinopterygians (bony fish) also increase greatly in diversity, but, unlike chondrichthyans, they begin small and remain small throughout the Mississippian. Thus, the trend is partially caused by small species leaving more (generally small) descendants rather than descendants typically being smaller than their ancestors. This might reflect higher speciation rates for small species (*5*), or small size "hitchhiking" along with elevated diversification happening for other reasons (*6*). Thus, selective extinction and differential diversification of actinopterygians (see the figure, panels C and D) plus driven trends and differential diversification of chondrichthyans (see the figure, panels B and C) drive the overall trend, with other vertebrates being mere onlookers.

As Sallan and Galimberti stress, there are no obvious correlations with extrinsic variables frequently linked to body size. Long-term trends toward cooler global temperature began after the polyphyletic trend toward increasing size but before that trend ceased. Similarly, there is no obvious association between the trends and atmospheric oxygen levels. Sampling controls (*7*) mean that preservational biases against finding small vertebrates in the Late Devonian or large vertebrates in the Mississippian cannot account for the pattern. Instead, Sallan and Galimberti suggest that size trends reflect trends in life-history traits, such as generation time, that are correlated with size. Thus, the distinction between sorting and selection (*8*) becomes important: The trends we see in a fossilizable trait (size) represent sorting of that trait based on selection for an associated unfossilizable trait (life history). Thus, the true role of size might be akin to the "stars" versus "no stars" in panel C in the figure: a trait that is largely (but not entirely) tied to another trait by functional or developmental association (or even simply because of common ancestry) (*7*) and that "hitchhikes" along the main trend.

In addition to offering a model for different types of trends, Sallan and Galimberti's work offers two important lessons for research concerning extant taxa. The first is the importance of sampling taxa over time. Suppose a time traveler deposited molecular phylogeneticists in the Mississippian and set them with the task of reconstructing the history of body size among (then) extant vertebrates. Shifting trends make reconstructing ancestral conditions extremely difficult without fossil data (*9–11*). Moreover, inferring diversity lost to extinction is generally very difficult given phylogenies of species from just one point in time (*12*). Without fossils, we cannot expect to see indications of when evolutionary parameters themselves changed. Indeed, it goes beyond stating that we need fossils to properly appreciate evolution among extant taxa: We need Devonian fossils to properly appreciate the evolution of subsequent Mississippian taxa.

The second lesson concerns current extinctions. Extinctions in the Late Pleistocene (~126,000 to 12,000 years ago) have preferentially eliminated large mammals (*13*). Large mammals have evolved many times, so it might seem that we should expect them to reevolve in the future. The differences between trends in the Devonian and Mississippian show that we cannot count on the trends of the past being the trends of the future. Thus, if conserving ecological and functional diversity is a priority as well as conserving phylogenetic diversity, then we cannot assume that large animals will quickly reevolve in the future. ■



Evolutionary trends. Different trends might underlie Devonian-Mississippian vertebrate evolution. Light colors denote small and dark colors, large body sizes. (**A**) In a passive trend, small species cannot become much smaller, but they can become much bigger (*2*). (B) In a driven trend, size increases are more common than size decreases (*3*). (**C**) Differential speciation means that large species live longer and/or have higher speciation rates (*4*). The stars/not-stars illustrate a hitchhiking trend in which differential speciation/extinction induces trends in other characters (*6*). (**D**) In the case of selective extinction, an extinction event (dashed line) inducing an immediate trend toward smaller taxa despite signs of the opposite trend before the event (*5*). [Figure adapted from (6)]

ILLUSTRATION: P. HUEY/*SCIENCE*

REFERENCES

1. L. Sallan, A. K. Galimberti, *Science* **350**, 812 (2015).
2. S. J. Gould, *J. Paleont.* **62**, 319 (1988).
3. D. W. McShea, *Evolution* **48**, 1747 (1994).
4. D. Jablonski, *Science* **231**, 129 (1986).
5. S. M. Stanley, *Proc. Natl. Acad. Sci. U.S.A.* **276**, 56 (1975).
6. P. J. Wagner, *Evolution* **50**, 990 (1996).
7. D. J. Bottjer, D. Jablonski, *Palaios* **3**, 540 (1988).
8. E. S. Vrba, S. J. Gould, *Paleobiology* **12**, 217 (1986).
9. J. A. Finarelli, A. Goswami, *Evolution* **67**, 3678 (2013).
10. J. A. Finarelli, J. J. Flynn, *Syst. Biol.* **55**, 301 (2006).
11. G. J. Slater, *Methods Ecol. Evol.* **4**, 734 (2013).
12. L. H. Liow *et al.*, *Syst. Biol.* **59**, 646 (2010).
13. S. K. Lyons *et al.*, *Evol. Ecol. Res.* **6**, 339 (2004).

10.1126/science.aad6283

Science

One era you are in—the next you are out

Peter J. Wagner

Science **350** (6262), 736-737.
DOI: 10.1126/science.aad6283